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DISTRIBUTIONAL PATTERNS OF *CECROPIA* (CECROPIACEAE): A PANBIOGEOGRAPHIC ANALYSIS

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Resumen

Con base en la distribución de 60 especies del género *Cecropia*, se hizo un análisis panbiogeográfico. Se construyeron 8 trazos generalizados con base en el patrón de distribución de 36 especies; la distribución de las demás especies no aportaba información para la definición de los trazos. La región andina tiene la mayor concentración de especies de *Cecropia* representada por la presencia de tres trazos generalizados y dos nodos; los dos trazos con mayor número de especies se localizan en su parte norte, en Colombia y Ecuador y el otro en los Andes centrales en Perú. Se encontraron además, cuatro trazos extrandinos: dos en la región amazónica, en Pará-Guayana y en Manaus, uno en Roraima, uno en Serra do Mar en la Selva Atlántica del Brasil y uno en Centro América. La especiación en *Cecropia* parece estar relacionada con el primer levantamiento de los Andes.

Palabras clave: *Cecropia*, biogeografía, Andes, Cecropiaceae, distribución de plantas.

Abstract

A panbiogeographic analysis of the distributional patterns of 60 species of *Cecropia* was carried out. Based on the distributional ranges of 36 species, we found eight generalized tracks for *Cecropia* species, whereas distributional patterns of 24 species were uninformative for the analysis. The major concentration of species of *Cecropia* is in the Neotropical Andean region, where there are three generalized tracks and two nodes. The northern Andes in Colombia and Ecuador are richer than the Central Andes in Perú, they contain two generalized tracks; one to the west and another to the east, formed by individual tracks of eight species each. There are four generalized tracks outside the Andean region: two in the Amazonian region in Guayana-Pará and in Manaus, one in Roraima, one in Serra do Mar in the Atlantic forest of Brazil and one in Central America. Speciation in *Cecropia* may be related to the Andean first uplift.

Key words: *Cecropia*, Biogeography, Andean, Cecropiaceae, plant distribution.

Introduction

Cecropia (Cecropiaceae) is a Neotropical genus comprising 60 species mainly of humid areas between sea level and 2600 m elevation. Species of *Cecropia* occur from southern Mexico to northern Argentina. The taxonomy of the genus is under investigation. There are several treatments for local floras such as Brazil (Berg 1978), Costa Rica (Standley 1937, Burger 1977), Perú (Macbride 1937), Venezuela (Velázquez 1972), the Guianas (Berg 1992), and Ecuador (Berg & Franco 1993).

The species of *Cecropia* are among the most conspicuous pioneer trees in natural gaps in primary forest of the Andean region, as well as in the tropical regions of the Pacific and Amazonian forests. They are also characteristic trees of secondary vegetation in disturbed places such as exposed riverbanks, landslides and along roadsides.

The information on the distribution of *Cecropia* is dispersed in herbarium labels and local floras. When preparing the monograph of the genus for Flora Neotropica, we found that there is enough information in collections to offer a more detailed treatment of the distributional patterns of the genus, which can help to understand the origin and distribution of this important element of the Neotropical flora.

The interest in the panbiogeographic approach (Croizat 1958 1964) has been revived and amplified through research programs in the seventies concerning the biogeographic problem of New Zealand (Grehan 1991), and its role in biodiversity and conservation studies (Grehan 1993). In Morrone & Crisci's (1995) sense, the panbiogeographic analysis can be used as a first step to establish general patterns and spatial homologies, and, as pointed out by Mayr (1978), as an additional source of interpretation. Generalized tracks indicate the possibility of preexistence of ancestral biotas, which become fragmented by tectonic or climatic changes (Morrone & Crisci 1995). The intersection of two or more generalized tracks produce nodes, which are considered to represent diversity centers known as hotspots (Grehan 1993).

We present here a panbiogeographic analysis of the distributional patterns of *Cecropia* species in order to identify areas to be used for a cladistic biogeographical analysis when the phylogeny of the genus becomes better understood.

Material and Methods

The analysis was based on the distributional data for 60 species of *Cecropia*. Data were taken from ca. 2800 specimens studied for the treatment of *Cecropia* for Flora Neotropica (Berg & Franco ms.) from the following herbaria: A, AAU, BG, COL, CTES, F, GB, GH, GUA, HUA, LOJA, LP, LPB, MA, MEDEL, MO, NY, P, PMA, PSO, Q, QCA, QCN, SCZ, SELBY, TEX, TULV, TUR, U, US and VALLE (acronyms follow Holmgren et al. 1981).

Localities were plotted on the Flora Neotropica base map; the localities of each species were connected by the shortest line to draw individual tracks; the overlap of specific tracks resulted in generalized tracks (Croizat 1958). We disregarded for the analysis the species represented by one or two nearby localities, species represented by isolated individual tracks and the widely distributed species.

Results

The individual tracks for each *Cecropia* species are shown in figures 2-12. There are eight species represented in only one or two nearby localities (fig. 2): *C. annulata*, *C. elongata*, *C. goudotiana*, *C. granvilleana*, *C. idroboi*, *C. multisecta*, *C. pittieri* and *C. silvae*. There are seven species represented by isolated individual tracks (fig. 5). These include: *C. litoralis*, with a geographical distribution from the Pacific coast to the Amazonian region at the Ecuador-Colombia border, and *C. polyphlebia* with a disjunct pattern, *C. mutisiana* and *C. sararensis* from the eastern cordillera of Colombia, *C. saxatilis* from the Cerrado of Brazil, *C. schreberiana* in the Antilles and *C. sylvicola* from Central America. The nine widely distributed species (fig. 3-4), *Cecropia angustifolia*, *C. distachya*, *C. concolor*, *C. engleriana*, *C. ficifolia*, *C. latiloba*, *C. membrancea*, *C. pachystachya*, *C. sciadophylla* and *C. telenitida*, were not included in the generalized tracks because they do not help to define the resolution of the tracks. Other widely distributed species, such as *Cecropia peltata* and *C. obtusifolia*, form part of a generalized track.

Based on the distributional ranges of the remaining 36 species, eight generalized tracks resulted (fig. 1):

1. Western Andean generalized track (fig 1.1). Located on the Pacific side of the western Andes of Colombia and Central Cordillera in Ecuador, it extends to the northern border of the Amotape-Huancabamba zone. It comprises the individual tracks of eight species: *Cecro-*

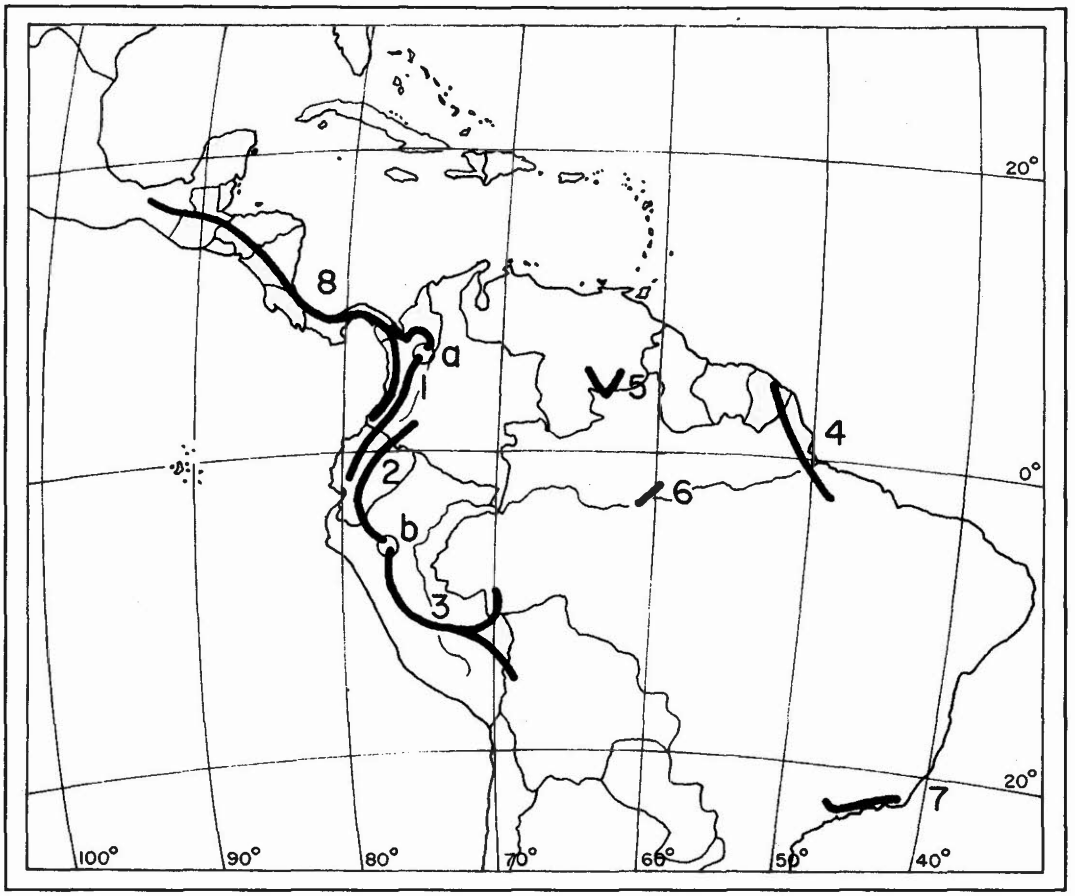

Figure 1. Generalized tracks. 1. Western Andean generalized track. 2. Eastern Andean generalized track. 3. Central Andean generalized track. 4. Guayana-Pará generalized track. 5. Roraima generalized track. 6. Manaus generalized track. 7. Serra do Mar generalized track. 8. Central America generalized track. a. Northwestern Colombian node b. Northern Perú node

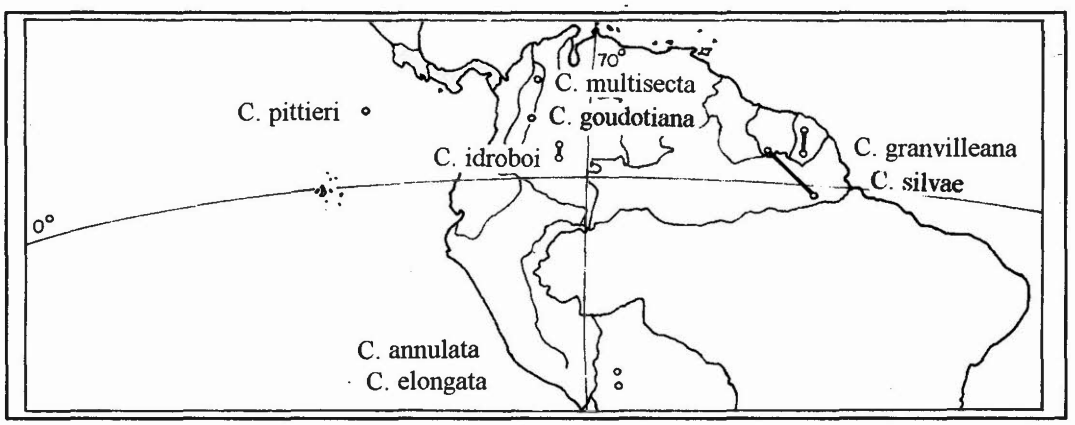

Figure 2. Species represented in only one or two nearby localities.

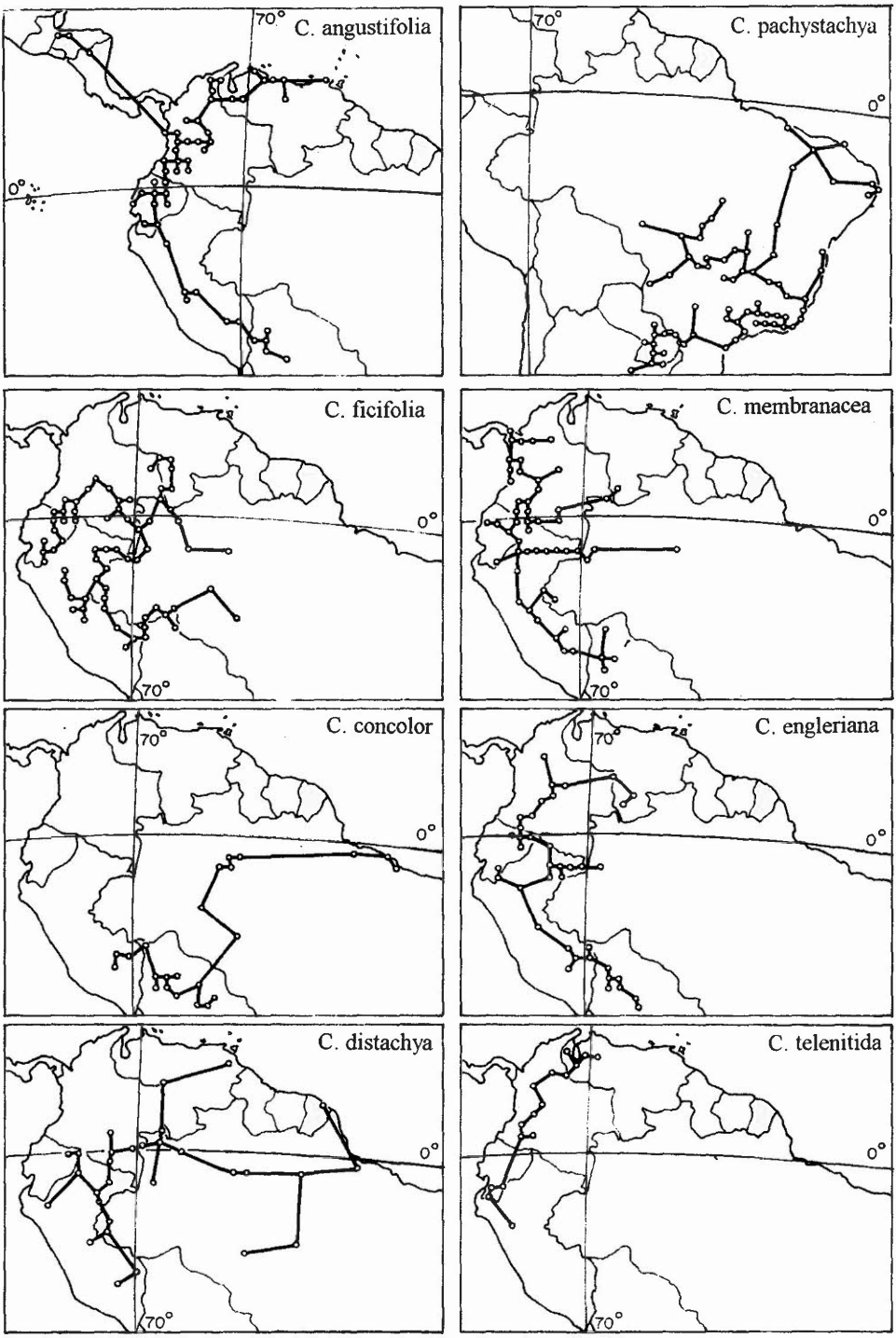

Figure 3. Individual tracks of the widely distributed species.

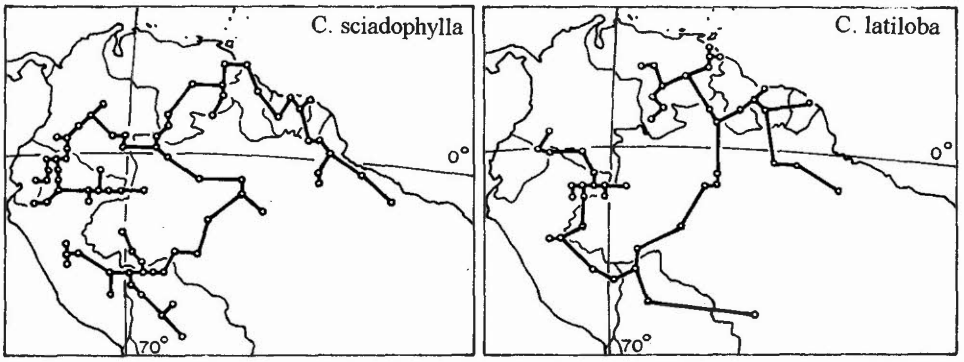

Figure 4. Individual tracks of the widely distributed species.

pia bullata, C. gabrielis, C. hispidissima, C. maxima, C. megastachya, C. plicata, C. reticulata and *C. telealba* (fig. 6).

2. Eastern Andean generalized track (fig. 1.2). Southeastern Cordillera of Colombia and Central Cordillera in Ecuador, running beyond the limit of the Amotape-Huancabamba zone. It includes the tracks of eight species: *Cecropia andina, C. herthae, C. marginalis, C. montana, C. pastasana, C. putumayonis, C. utcubambana* and *C. velutinella* (fig. 7).

3. Central Andean generalized track (fig. 1.3). In the Central Cordillera of Perú. It is constructed from five individual tracks including: *Cecropia albicans, C. polystachya, C. puberula, C. strigosa* and *C. tacuna* (fig. 8).

4. Guayana-Pará generalized track (fig.1.4). It consists of two species, *Cecropia obtusa* and *C. palmata* linking eastern Surinam and Pará in Brazil (fig. 9).

5. Roraima generalized track (fig. 1.5). Includes *Cecropia kavanayensis* and *C. angulata* (fig. 10).

6. Manaus generalized track (fig.1.6). In the central Amazonian region. It consists of the individual tracks of *Cecropia ulei* and *C. purpurascens* (fig. 11).

7. Serra do Mar generalized track (fig. 1.7). In southern Brazil, in the Atlantic forest. It consists of the individual tracks of *Cecropia glaziovii* and *C. hololeuca* (fig. 11).

8. Central American generalized track (fig. 1.8). Extending from southern Mexico to the Chocó biogeographic area of Colombia, it runs down into the wet valleys of the Cauca and Magdalena rivers in Colombia. It comprises seven tracks: *Cecropia garciae, C. heterochrona, C. insignis, C. longipes, C. obtusifolia, C. peltata,* and *C. virgusa* (fig. 12).

There are two nodes; (a) one in northwestern Colombia where the generalized track from Central America and the western track intersect; and (b) the second in northern Perú, where the two tracks of the Central Andes intersect (fig. 1).

Discussion

The distributional patterns found in *Cecropia* are very similar to the congruence or nuclear areas delimited by Müller (1973) based on distributions of terrestrial vertebrates. In Cabrera & Willink's (1973) biogeographic proposal for Latin America, the species of *Cecropia* belong mainly to the Amazonian domain. There is only one species from the Caribbean domain (C. *schreberiana*) and one

endemic to the Guayana domain (*C. kavanayensis)*. Although the Amazonian and Roraima generalized tracks are weakly supported (two species each), note that their presence coincides with the distributions of other organisms (Müller 1973).

The ecological preferences (humid areas) of *Cecropia* species and their altitudinal limits (below 1000 m alt.) in Central America put them into the Pacific province of Cabrera & Willink (1973). We prefer this circumscription instead of splitting them into several of the seven centres proposed by Müller (1973). *Cecropia peltata* is the only species linking Central America to the Caribbean islands (Jamaica), and it is morphologically related to *C. schreberiana*, represented by an isolated track on the Antilles.

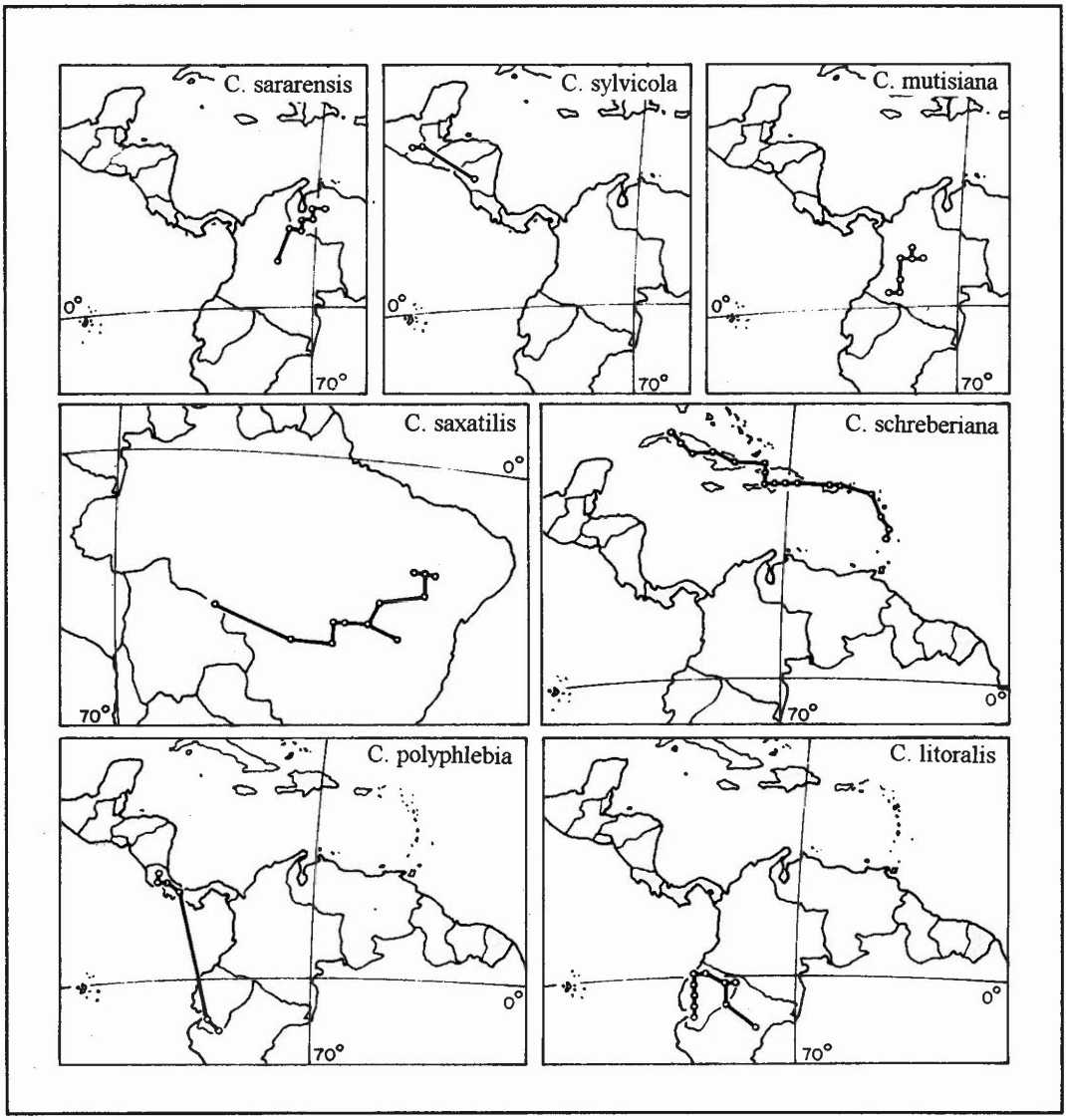

Figure 5. Species represented by isolated individual tracks.

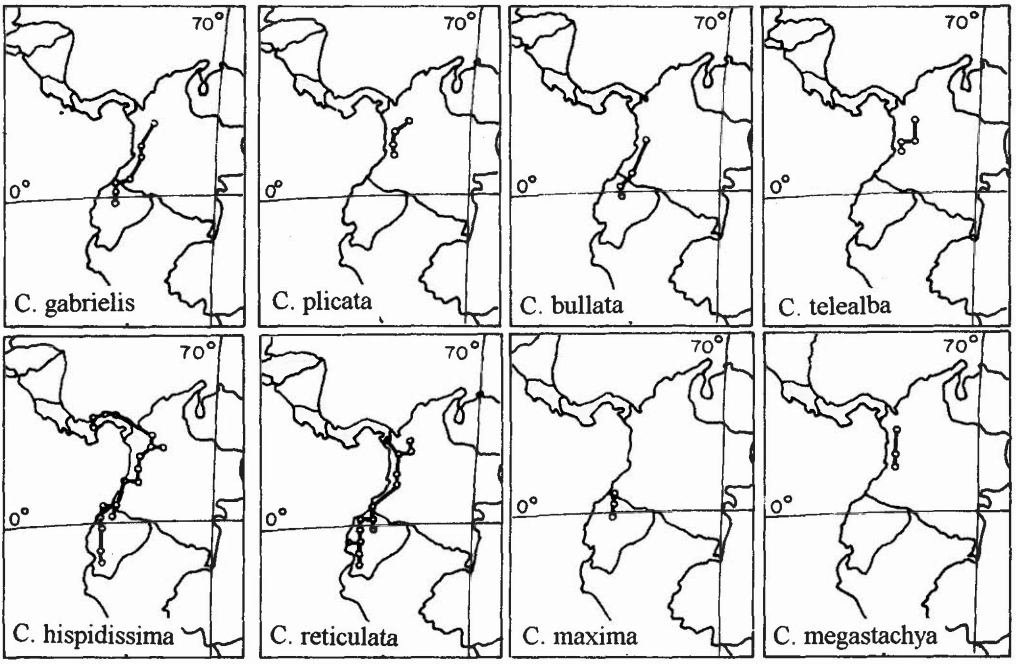

Figure 6. Individual tracks of the eight species of the Western Andean generalized track.

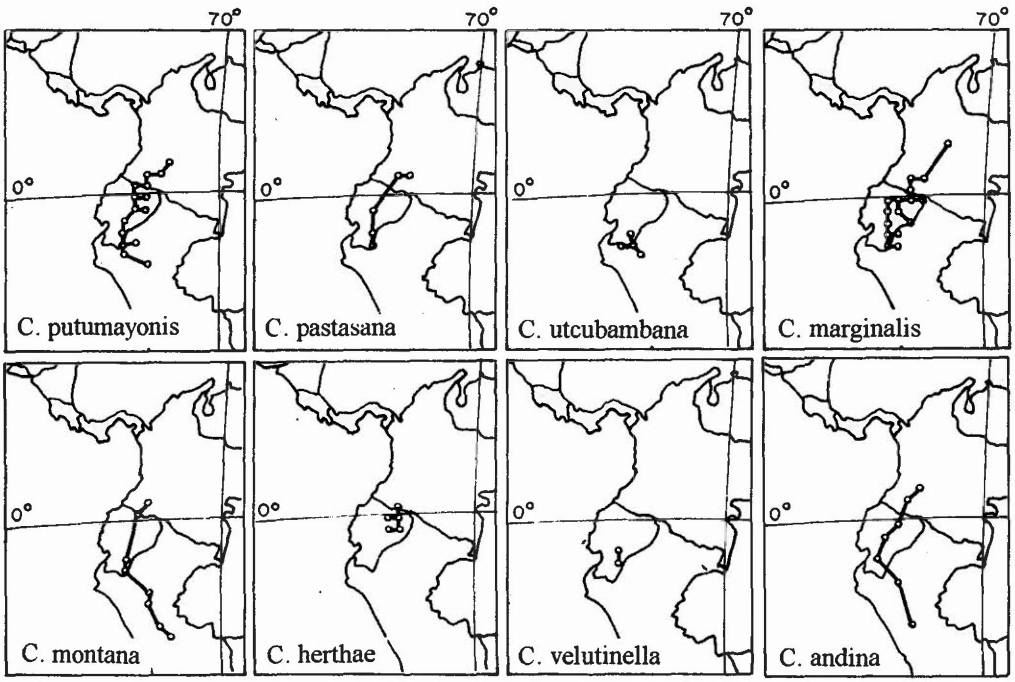

Figure 7. Individual tracks of the eight species of the Eastern Andean generalized track.

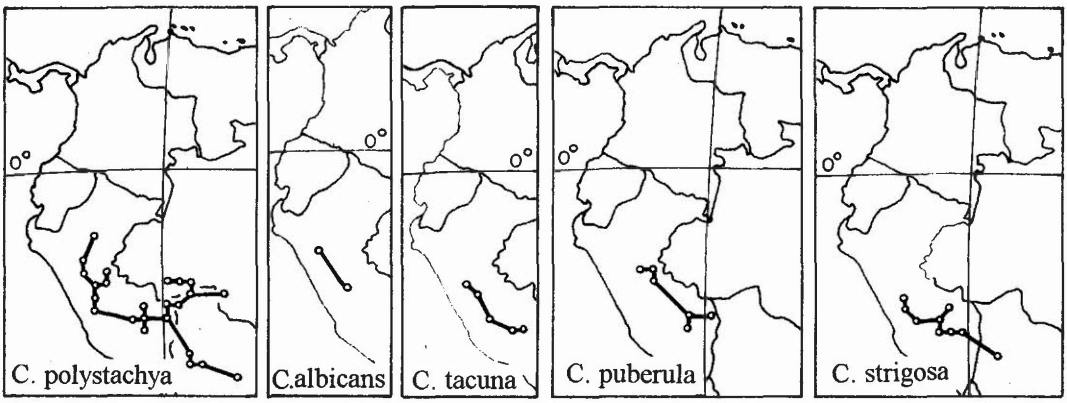

Figure 8. Individual tracks of the five species of the Central Andean generalized track.

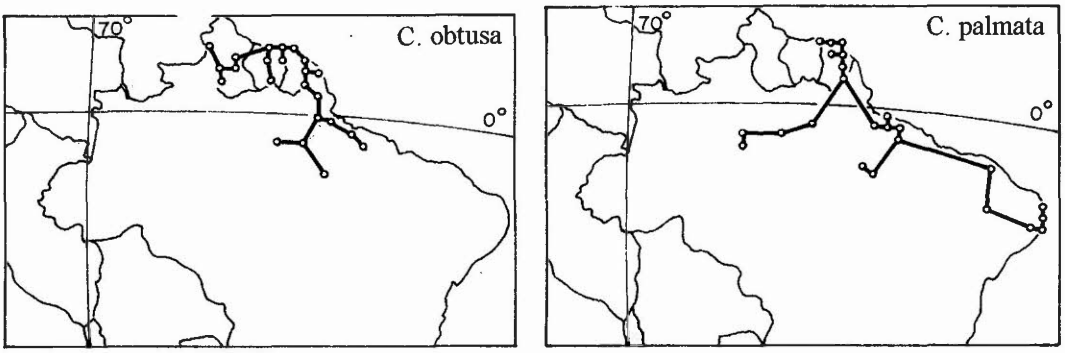

Figure 9. Individual tracks of the two species of Guayana-Pará generalized track.

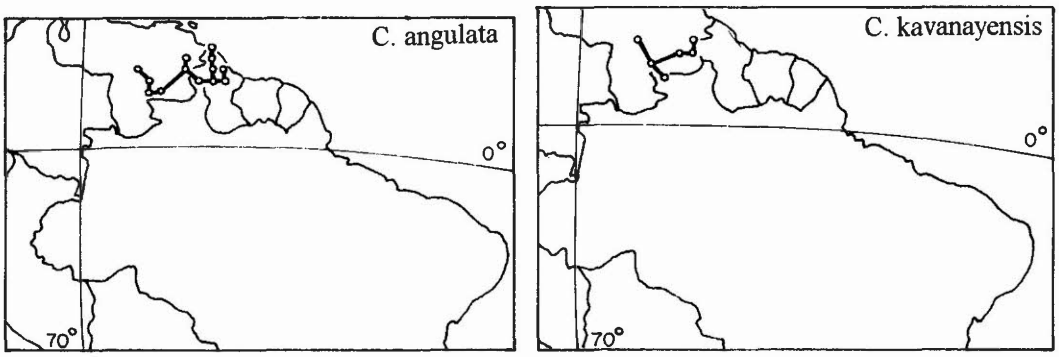

Figure 10. Individual tracks of the two species of Roraima generalized track.

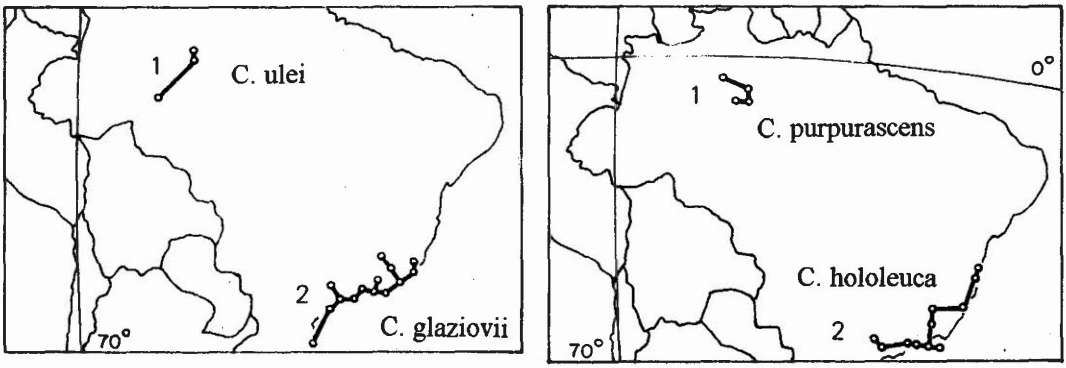

Figure 11. Individual tracks of the species of Manaus (1) and of Serra do Mar (2) generalized tracks.

The generalized track in the Atlantic province (7) of Cabrera & Willink (1973) is located within the limits of the Serra do Mar centre of Müller (1973) at the Paulista subcentre, represented by the generalized track formed by the *Cecropia hololeuca* and *C. glaziovii* tracks; these species are isolated from the rest of the species of the genus. *Cecropia glaziovii* is morphologically closer to C. *palmata* from the Guayana-Pará centre.

The distribution of *Cecropia saxatilis* fits into the Cerrado province and Campo Cerrado centre of Brazil, there is no connection between its distribution and the geographically closest species of Serra do Mar centre. Morphologically the species is related to *Cecropia palmata* of the Guayana- Pará centre and to *C. glaziovii* of the Serra do Mar centre. The individual track of *Cecropia pachystachya* overlaps some points of Serra do Mar and Campo Cerrado tracks.

The main massing for *Cecropia* is the Andean region because it has the major concentration of species, which are represented by three generalized tracks and two nodes. The distribution is coincident with the centres of Müller (1973). The Central Andes generalized track (3) of Perú is equivalent to the Yungas centre of Müller, and extends to the Pisco or Abancay reflection mentioned by BERRY (1982) as a division of the Central Andes. It meets the Eastern Andes generalized track (2) in the southern node located in northeastern Perú. That node is placed at a lower latitude than the Amotape- Huancabamba zone considered as the transitional area linking the Northern and Central Andes (Berry 1982). The eastern and western Andean generalized tracks mostly correspond to the Colombian montane forest centre of Müller (1973): the former to the east Andean subcentre and the latter to the Colombian west Andean subcentre. The northern node is located in the lower Magdalena valley in Colombia, close to the end of the Cordillera Central at the Nechi subcentre (Müller 1973), which is a point of confluence of Chocoan and Amazonian floras. The isolated track of *Cecropia polyphlebia* (fig. 2) may be related to the position of the Panama-Costa Rica island arc since the beginning of the tertiary (Taylor 1995). There is no generalized track for the Chocó as in other groups (Gentry 1982, Lourenço & Flores 1990), although there are individual tracks present there.

The Andean species are connected to the central Amazonian region by *Cecropia* species of wide distribution, such as *C. sciadophylla*, C. *latiloba* and *C. distachya*. *Cecropia membranacea* is the only species widespread in the Pacific and Amazonian regions. The Amazonian *Cecropia* species have a wide east-west distribution and in several places overlap the

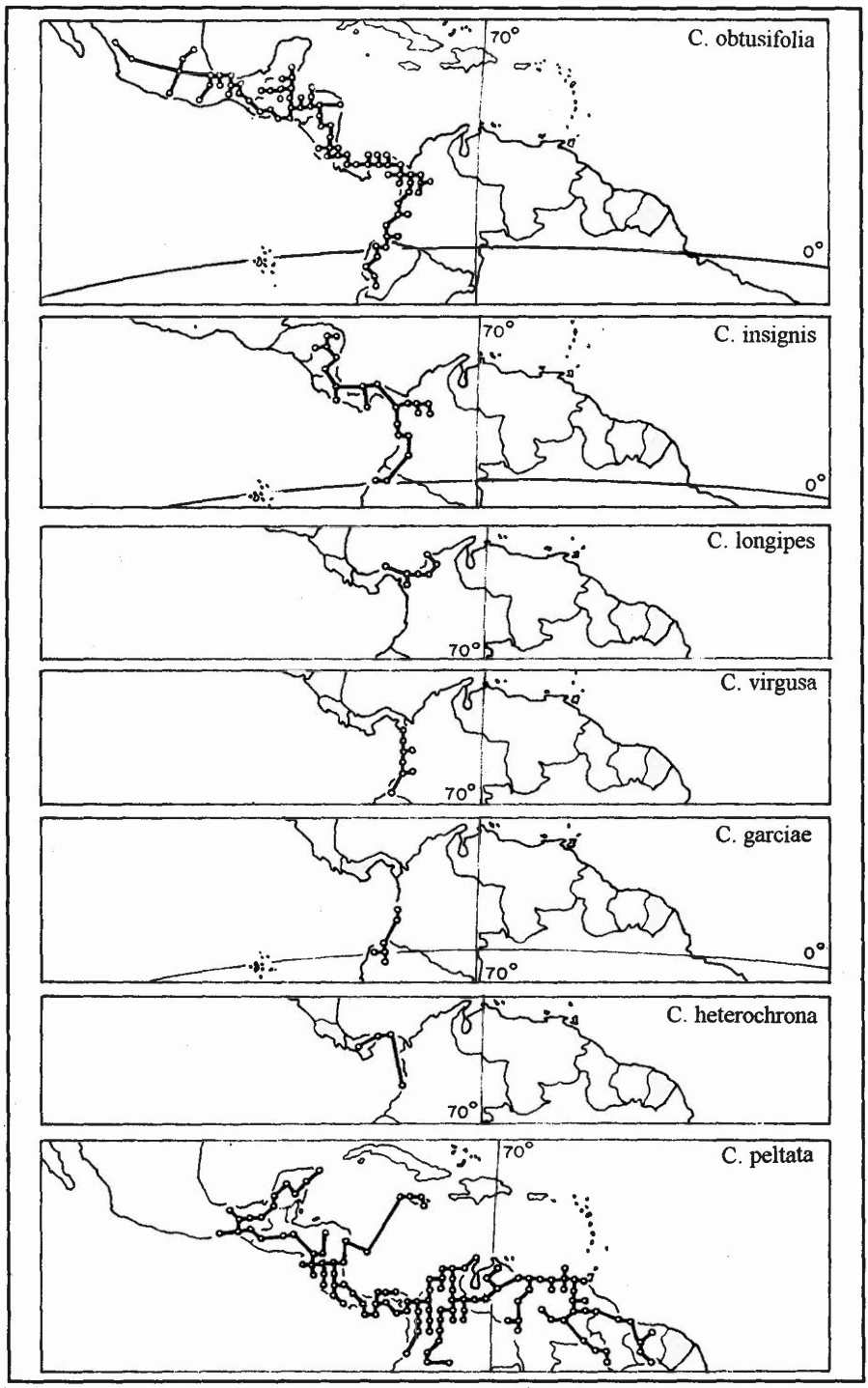

Figure 12. Individual tracks of the seven species belonging to the Central America generalized track.

eastern and central generalized tracks in central and northern Andes where they increase the diversity of species.

The main distributional patterns within the Andes are related to the uplift of the cordilleras, where most of the *Cecropia* species tracks stand. The high concentration of *Cecropia* species in the Western Cordillera is probably influenced by its latter uplift and as it makes a contact point with Central America rather than with the other Andean areas, the speciation of the genus there seems to be relatively recent. The eastern and central tracks intersect below the Amotape-Huancabamba region which has an older history related with the collision of the Nazca and the South American plates (Simpson 1979). The Central America generalized track supports a rather recent interchange between the northern South America and Meso-America paleofloras as suggested by Taylor (1995), but there are no pollen records from the Miocene, Pliocene (Graham 1991), or even Eocene (Graham 1985) in paleobotanical studies from Panamá.

The generalized tracks of *Cecropia* species suggests that *Cecropia* is an Andean centered genus. There are several palynological and fossil seed records of *Cecropia* in the high plain of Bogotá from the Miocene (Wijninga 1996). Speciation in the Andes may be attributed to the Andean first uplift of previously lowland forms in the northwest of South America. The resulting areas obtained from the generalized tracks can be used as preliminary areas in search of areas of endemism in studies of vicariance analysis for *Cecropia* and similar distributional groups.

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